BLACK AND PALE SWALLOW-WORT (VINCETOXICUM NIGRUM AND V. ROSSICUM) SITES IN NORTH AMERICA AND THE IMPACT OF ABIOTIC SOIL FACTORS ON THEIR OCCURRENCE AND GROWTH

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ABSTRACT

The alien invasive vines, black and pale swallow-wort are currently spreading across eastern North America, invading parklands, old fields, restored forest sites, and other natural areas. These plants spread by wind-borne seed and can form dense stands where they become established. Their current ranges remain distinct with little overlap; however, it is unclear how much further their ranges are likely to expand and whether their ranges will eventually overlap. Availability of this information will be valuable for the management of these two species, especially in the context of biological control. Light availability has been shown to impact swallow-wort growth and fecundity, but the effects of other abiotic factors such as soil characteristics have not been examined. Preliminary observations and anecdotal information have associated black swallow-wort with low-pH, low-fertility soils and pale swallow-wort with high-pH, high-fertility soils. We conducted a soil sampling and site mapping study, a field experiment, and a growth chamber experiment to determine the impact of abiotic soil factors on the occurrence and growth of both swallow-wort species.

The soil sampling study provided an overview of habitat and soil characteristics found in areas colonized by the swallow-worts. Location data, site descriptions, and soil samples were collected from areas occupied by the swallow-worts from their introduced range. A total of 27 soil samples were analyzed for black swallow-wort and 68 samples for pale swallow-wort. Contrary to the expectation that either species would be constrained to a narrow soil pH range, both species were found on soils that ranged widely in pH (4.7-7.9). In general, pale swallow-wort tended to be found on higher fertility alfisols and black swallow-wort on lower fertility inceptisols, though both species occurred on a variety of soil types. The two species

were associated with minimally disturbed sites, especially the edges of trails and roadways, abandoned fields, and secondary growth forests. Our findings suggest that soil types across a range of pH are susceptible to invasion by these swallow-wort species; however, it was unclear whether growth and fecundity of these two invasive vines is similar across these various soil types and pH.

To determine if swallow-wort emergence and performance is affected by soil pH or soil type, we conducted a common garden field experiment during two years and a soil incubation growth chamber germination. In the common garden experiment, differences in growth varied primarily by species, with black swallow-wort plants having greater biomass and fecundity than pale swallow-wort plants. In the growth chamber experiment, species had no effect on the initial seed germination and emergence of seedlings. Soil pH (three levels in the field study, 12 levels in the growth chamber study) had minimal effects on swallow-wort growth. Soil type had some effect on stem height, with black swallow-wort growing taller than pale swallow-wort on a high-fertility soil, contrary to our original hypothesis. Pale swallow-wort had greater biomass allocation to roots than black swallow-wort, which is consistent with other studies. Overall, plant growth of the two swallow-wort species was vigorous for all soil type and soil pH treatment combinations suggesting that these two species can colonize and grow well in a relatively wide range of soil pH conditions. Thus, although their current ranges in North America do not appear to overlap substantially, this may not be due to these two invasive plants having narrow species-specific soil preferences as may have been postulated. From a management perspective, our results suggest that the current range of these two species is likely to continue to increase and that early detection rapid response (EDRR) programs should be established in susceptible regions not yet colonized by these two invasive vines.

BIOGRAPHICAL SKETCH

Lillian Charna Magidow was born to her mother, a clothing pattern-maker, and her father, an artist, in Santa Barbara, CA. At age ten she and her family moved to Hopkins, MN, and later to Minneapolis, MN where she graduated from South High School. Her favorite books inspired her to learn more about the edible and medicinal plants of Minnesota, which led to a lifelong fascination with the natural world. This was reinforced by many fun years spent attending and working at Camp Sunrise summer camp in Rush City, MN. While still in high school, she pursued another passion of hers, cooking, and studied Culinary Arts at Minneapolis Community and Technical College. During her studies an intensive environmental science course re-focused her on biology and sparked her interest in agriculture. She then transferred to the University of Minnesota College of Agriculture, Food, and Environmental Science, where she was awarded the Robert G. Robinson Undergraduate Scholarship to study Applied Plant Science with a minor in Sustainable Agriculture. While an undergraduate at the University of Minnesota, she traveled to Chiapas, Mexico with the Student Project for Amity among Nations program to conduct independent research. She investigated the impact of commodity trade policy on indigenous maize farmers, which ultimately became her undergraduate thesis. Her project was funded by the Theodora and Arnold A. Johnson Research scholarship for independent undergraduate research and the John D. Lindstrom Grant. As an undergraduate she held several student research assistant positions, which inspired her to further pursue science at the postgraduate level. She was named the ASA-CSSA-SSSA Outstanding Senior and graduated summa cum laude with distinction.

Lillian was admitted to the Cornell University Weed Ecology and Management Research Group, where she worked with Drs. Antonio DiTommaso, Lindsey Milbrath, and Quirine Ketterings. She was awarded the Cornell University Graduate Fellowship for her first year of study and received ongoing support from the USDA-ARS project for biological control of swallow-wort. Her research at Cornell focused on the biology and ecology of the alien invasive vines, black and pale swallow-wort, and the effects of soil properties on their growth and distribution. Lillian enjoys teaching, and while at Cornell she had the opportunity to be a teaching assistant for the Weed Science undergraduate course, to study science education, and to teach elementary school students at the Ithaca Community Gardens about weeds. She served as an officer in the Crop and Soil Science Graduate Student Association and received the MacDonald and Musgrave Award for Graduate Student Excellence. She attended the Northeastern Weed Science Society Annual Meeting, the Annual Collegiate Weed Science Contest, and presented her Master of Science research at the Weed Science Society of America (WSSA) Meeting in Chicago, IL in 2008.

She currently resides in Minnesota, where she is surrounded by family and friends. She hopes to continue working in invasive species research, management, and outreach in the region. She is still passionate about cooking and also spends time creating recipes, ballroom and Latin dancing, reading, and competing in Olympic weightlifting.

For my family.

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CHAPTER 1

SOIL CHARACTERISTICS OF NORTH AMERICAN SITES COLONIZED BY THE NON-NATIVE INVASIVE VINES BLACK AND PALE SWALLOW-WORT *(VINCETOXICUM NIGRUM* AND *V. ROSSICUM)*[*]

Introduction

Black swallow-wort (*Vincetoxicum nigrum* (L.) Moench.) (hereafter referred to as BSW) and pale swallow-wort (*Vincetoxicum rossicum* (Kleopow) Barbar.) (hereafter referred to as PSW) are two non-native, invasive perennial vines in the Apocynaceae that are becoming increasingly problematic in the northeastern United States (U.S.) and southeastern Canada (DiTommaso et al. 2005). Affected habitats include unique plant and animal alvar communities in the Lower Great Lakes Basin, old fields, ecotone areas, Christmas tree plantations, and reduced tillage cropping systems (DiTommaso et al. 2005; Douglass et al. 2009). These species can spread widely by wind-borne seed and by tillering from robust root crowns. Chemical and/or mechanical control can be effective for small, isolated populations (Averill et al. 2008; Lawlor and Raynal 2002; Mervosh and Gumbart 2006), but to control large swallow-wort infestations, an integrated approach is likely necessary including the use of biological control tactics (Carpenter and Cappuccino 2005; Douglass et al. 2009; Milbrath and Biazzo 2006). According to Shea and Possingham (2000), the effectiveness of any biological control program is limited by the extent and accuracy

[*] Coauthored with Antonio DiTommaso, Quirine M. Ketterings, & Lindsey R. Milbrath.

of knowledge about the underlying biology, ecology, and distribution of the target organism(s), but some of this basic knowledge about BSW and PSW is currently lacking (DiTommaso and Milbrath 2006). For instance, more information about which biotic and abiotic factors may influence the spread and performance of these species is needed.

In their native ranges in Europe, BSW and PSW are separated by hundreds of kilometers, growing in distinctly different climate zones and soil types (DiTommaso et al. 2005). In North America, however, both species are present throughout the Lower Great Lakes Basin, and although their ranges remain relatively distinct, they have been found within the same county (Milbrath and Biazzo 2006; Sheeley and Raynal 1996), and in isolated cases, at the same site (L. L. Smith, Cornell University, personal communication). BSW has been reported in 21 U.S. states, ranging from Maine to Minnesota and as far south as Kansas and Missouri (with an isolated population at the University of California, Riverside), and the Canadian provinces of Ontario and Quebec (DiTommaso et al. 2005; USDA, NRCS 2009). The range of PSW is more limited, including nine U.S. states and two Canadian provinces: Connecticut, Indiana, Massachusetts, Michigan, Missouri, New Hampshire, New Jersey, New York, Pennsylvania, Ontario, and Quebec. The North American range of PSW has expanded to roughly three times its European range within a century (Kricsfalusy and Miller 2008), and the range of BSW has expanded even more widely. Although previous studies have linked the occurrence of PSW with calcareous soils (Lawlor 2000), which contain higher levels of both calcium (Ca), and magnesium (Mg) than soils on which BSW occurs (Douglass 2008; Douglass et al. 2009), no systematic survey has been undertaken to verify if this association is accurate. Furthermore, BSW populations tend to occur on formerly forested inceptisols of southern NY State and New England, while PSW populations are frequently observed on fertile alfisols that form a narrow band across central NY State (L. C. Magidow, Cornell University, unpublished data).

Abiotic factors such as soil characteristics play a critical role in plant invasions (Gerhardt and Collinge 2007) and the distribution of species across the landscape (Dunson and Travis 1991), but are studied less frequently than biotic factors (Holway et al. 2002; Moyle and Light 1996). To date, only a few studies have examined the role of abiotic factors on growth and fecundity of the swallow-worts in their introduced range and these have focused on the effects of light availability (Hotchkiss et al. 2008; Milbrath 2008; Smith et al. 2006). No studies have attempted to systematically link the occurrence of these two swallow-wort species to soil types and soil pH.

One method of examining the link between the distribution of invasive species and the abiotic characteristics of the habitats they invade is through the use of spatial analysis within a geographic information system (GIS). The use of GIS technologies in invasive biology and management research has increased rapidly during the last decade (Holcombe et al. 2007; Meyerson and Reaser 2003). This approach is most commonly used with quantitative data, but qualitative methods of habitat evaluation can be a fast and cost effective way to inform future experimentation, and can be combined with quantitative methods to create a comprehensive approach to research and management (van Lanen et al. 1992).

The objective of this study was to use site descriptions, soil chemical analysis, and spatial analysis to determine whether PSW and BSW are associated with specific soil types and soil pH in their introduced North American range. We hypothesized that BSW would be found primarily in low pH soils and inceptisols and PSW in higher pH soils and alfisols.

Materials and Methods

To obtain soil samples from as wide a geographic range colonized by the two swallow-wort species as possible, we contacted individuals that were familiar with these invasive species in their range in the northeastern U.S. or Canada. A total of 24 participants agreed to provide soil samples from locations where the swallow-worts were present. Participants were provided with a soil sampling protocol and a questionnaire. The questionnaire asked for the specific location of each sample site (longitude and latitude, GPS coordinates, or street address) and the swallow-wort species found at this location. Information about the land use history of the area, if known, and the degree of disturbance at the site were also requested. At each sample location, participants were also asked to estimate the area colonized by the swallow-wort species and to estimate the percent cover it occupied. Lastly, at the time of sampling, participants were requested to estimate the phenological stage of the majority of swallow-wort plants (e.g. vegetative, flowering, follicle set, or follicle dehiscence), and to list the dominant plant species at each site. If participants were unable to determine the swallow-wort species present at their site, they were instructed to mail a voucher specimen to the authors so that an accurate identification of the species was made.

Participants were instructed to collect 10 to 20 soil cores from each site and create a composite sample before mailing to Cornell University for chemical analysis. Each soil core was taken using a soil probe or garden spade by clearing surface vegetation at each location, and digging a 2.5 by 1.5 by 15 cm deep soil slice. Upon receipt, soil samples were oven-dried at 32 C for 24 h. Samples were ground to pass through a 2 mm sieve and analyzed for Morgan extractable P, K, Ca, Mg, Fe, Al, Zn, Mn and Al (Morgan 1941), using an automated rapid flow analyzer[1] for Morgan extractable P and an inductively coupled plasma spectrophotometer (ICP)[2] for all other elements. Soil pH was determined using a 1:1 soil:water ratio. Organic matter (OM) was determined using loss-on-ignition with 2 h exposure to 500 C as described in Storer (1984). Percent OM was calculated from loss-on-ignition (LOI) using the following formula: % OM = (%LOI x 0.7) – 0.23 (R. Rao, Cornell University, personal communication, 2007). All analyses were conducted at the Cornell Nutrient Analysis Laboratory (CNAL) using the standard procedures described in Sims and Wolf (1995).

Soil data for GIS spatial analysis were obtained from the State Soil Geographic (STATSGO) database for NY State at the Cornell University Geospatial Information Repository (CUGIR) (Cornell University 2009). Spatial analysis was conducted in Manifold System 8.0 (Manifold Net, Ltd. 2009) and cartography was performed using the ArcGIS 9.2 program (ESRI 2006). State and county polygons for the United States were extracted from the U.S. Census Bureau's Master Address File/Topologically Integrated Geographic Encoding and Referencing (MAF/TIGER) database in the form of TIGER/Line Shapefiles (U.S. Census Bureau 2008), and Canadian provinces were added from the National Weather Service Canadian Provinces and Territories Shapefile (National Weather Service 1999). The STATSGO layer data used for the analyses included the NY State boundaries and polygons, the soil survey map units, and the associated soil types (from NY, MAPUNIT, and TAXCLASS layers respectively). 'Map units' are land areas comprising similar soil components representing several soil series (NRCS 1994).

[1] Alpkem, RFA/2-320, OI Corp., College Station, TX.
[2] JY70 Type II-AES, Jobin Yvon Inc., Edison, NJ.

Soil test results were analyzed in two separate sets: (1) results from all sample sites, and (2) results from NY State only. Median soil pH values and their range were reported for both species within these sets. The remaining soil characteristics were subjected to normality analysis using JMP 7.0 statistical program (SAS Institute, Inc. 2007). Parameters with a skewness or kurtosis greater or less than ± 3 (which included P, Mg, Fe, Al, Zn, and Cu) were log transformed or arcsine square-root transformed (% OM) to achieve normality. Soil parameter means for BSW and PSW were compared using one-way ANOVA, with a significance level of $\alpha = 0.05$. Due to different sample sizes between species, equal variance could not be assumed. Thus, each dataset was tested for unequal variance using Levene's test, and the Welch ANOVA *P*-value for unequal variance was reported. Qualitative survey data were examined to detect any notable differences between species.

Results and Discussion

Soil Samples. The 24 participants provided a total of 95 soil samples, 27 from BSW sites and 68 from PSW sites. Samples were collected in six U.S. states (CT, MA, NY, PA, RI, and VT) and one Canadian province (Ontario). The majority of samples were collected in NY State (n= 66).

The median soil pH for all locations was 6.2 for BSW (n= 27) and 6.9 for PSW (n= 68) (Table 1.1). The pH range for both species was wide; with BSW found on soils with a pH range from 4.7 to 8.0, while the pH of soils on which PSW was found ranged from 4.7 to 7.9. These findings do not support our hypothesis that BSW plants would be found on relatively low pH soils and PSW plants found on relatively high pH soils. The soil fertility of sampled sites differed by swallow-wort species. In general, PSW was found on soils with greater available concentrations of P, K, Ca, and Mg, and higher organic matter content. Levels of Al and Zn were higher in soil colonized by BSW, whereas Cu and Mn were higher at PSW sites, and Fe concentrations did not differ by species (Table 1.1). These results are consistent with our hypothesis that PSW plants typically occur on richer, more fertile soils relative to soils colonized by BSW.

Within NY State sites, the median soil pH was 6.5 for BSW (n= 12) and 7.0 for PSW (n= 54) (Table 1.2). Soils colonized by BSW encompassed a pH range from 5.2 to 8.0 while soils colonized by PSW ranged in pH from 4.4 to 7.9. Thus, consistent with results for the entire soil sample data set, our hypothesis that PSW would be associated with high pH soils (pH > 7.0) and BSW with low pH soils (pH < 5.0) was not supported. For NY State samples, soils colonized by PSW had higher organic matter content and concentrations of P, K, Mg, Ca, and Mn than soils colonized BSW. The remaining elements did not differ between the two species (Table 1.2).

Soil Classification. Of the map units dominated by alfisols, 97% were colonized by PSW, although this species also occurred in map units dominated by entisols, histosols, and spodosols (Table 1.3). Alfisols have a relatively high inherent fertility and clay content. They were typically formed under forests, and in NY State they occur in a wide band across the southern shore of Lake Ontario (Brady and Weil 2002).

Entisols are a diverse group of soils characterized by little structure or development, often formed by the eroding or mixing of surrounding materials. Histosols are organic soils which are formed over peat bogs or muck. Spodosols are acidic, sandy soils that typically formed under coniferous forests. The majority of sites in which BSW occurred was characterized as inceptisols (67%), although both species

Table 1.1. Soil test results for all 95 samples where the swallow-worts were found. Data provided include median soil pH and range (minimum, maximum), mean soil parameter including standard deviation (SD) and standard error (SE), and the probability that the relationships between each soil characteristic and each of the swallow-wort species are significant[ab].

	Black Swallow-wort (n = 27)			Pale Swallow-wort (n = 68)			
Soil Parameter	Median	Range		Median	Range		
pH	6.2	(4.7, 8.0)		6.9	(4.4, 7.9)		
	Mean	SD	SE	Mean	SD	SE	
Organic matter (%)	3.59	1.58	0.30	6.77	6.91	0.84	**
P (mg kg^{-1})[c]	4.6	4.7	0.9	13.6	22.0	2.7	**
K	73	36	7	106	70	9	**
Mg	122.9	71.3	13.7	197.0	197.1	23.9	**
Ca	1932	2001	385	4842	5072	615	**
Fe	5.8	3.2	0.6	6.5	9.2	1.1	n.s.
Al	61.6	52.3	10.1	32.5	30.9	3.7	*
Mn	16.5	12.2	2.4	27.5	18.7	2.3	**
Zn	4.53	5.47	1.05	2.22	2.05	0.25	*
Cu	3.1	2.6	0.5	7.2	8.7	1.1	*

[a] Mean values tested for differences between species using Welch-ANOVA test for unequal variance, $\alpha = 0.05$.

[b] * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$, n.s. = not significant.

[c] (mg kg^{-1}) unit for other parameters in list.

Table 1.1. Soil test results for New York state samples where the swallow-worts were found. Median pH value and range (minimum, maximum), mean soil characteristic standard deviation (SD) and standard error (SE), and the probability that the relationships between each soil characteristic and each species are significant[ab].

	Black Swallow-wort (n = 12)			Pale Swallow-wort (n = 54)			
Soil Parameter	Median	Range		Median	Range		
pH	6.5	(5.2, 8.0)		7.0	(4.4, 7.9)		
	Mean	SD	SE	Mean	SD	SE	
Organic matter (%)	2.90	1.41	0.40	7.40	7.57	1.00	**
P (mg kg^{-1})[c]	1.3	0.9	0.3	14.8	24.3	3.3	***
K	53	23	7	105	76	10	***
Mg	116.2	69.5	20.1	210.0	217.2	29.6	*
Ca	2439	2717	784	5368	5122	697	***
Fe	6.2	3.4	1.0	5.9	9.7	1.3	n.s.
Al	53.4	46.7	13.5	29.3	28.8	3.9	n.s.
Mn	18.5	12.8	3.7	30.0	19.2	2.6	*
Zn	2.53	2.83	0.82	2.04	1.96	0.27	n.s.
Cu	2.6	3.5	1.0	7.8	9.0	1.2	n.s.

[a] Mean values tested for differences between species using Welch-ANOVA test for unequal variance, $\alpha = 0.05$.

[b] * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$, n.s. = not significant.

[c] (mg kg^{-1}) unit for other parameters in list.

were observed in these soils. Inceptisols include young soils which have often formed on rocky areas or steep slopes, and are similar to entisols. Both species are capable of colonizing highly eroded soils, with 92% of BSW sites and 41% of PSW found in inceptisols and entisols. Based on our findings for NY State samples, PSW populations appear to occur in a wider variety of soil types than BSW populations. Our hypothesis that PSW would occur on alfisols and BSW on inceptisols was not supported unequivocally, although our results were consistent with this general pattern.

General Site Descriptions. Information provided by the 24 participants that collected soil samples varied widely. Although these data do not lend themselves to statistical analysis, some helpful patterns related to the type of sites colonized by the two swallow-wort species do emerge from the information collected. Since most of the sampling occurred in August and September 2007, the majority of swallow-wort populations were in the follicle fill or follicle dehiscence stage of growth, although plants from PSW populations were generally at a more advanced phenological stage. The size of swallow-wort patch sizes ranged from a few meters in diameter to a stand of PSW over 100 ha in size. In general, PSW populations occupied larger areas at sample sites than BSW populations. The percent cover of swallow-wort plants was also greater in PSW stands than BSW stands. Many of the sample sites colonized by swallow-wort had historically been used for agriculture, but have since reverted to secondary successional forests, old field trails or have been converted into residential areas, and no longer undergo frequent disturbance. This land-use pattern change is common in many regions of central NY State. The two swallow-wort species colonized a variety of habitats, from secondary old-growth hardwood forests to old fields as well as suburban lawns. Neither species was reported in row-crops or other systems undergoing frequent tillage. It is possible that the extensive row crop

Table 1.3. State Soil Geographic Database (STATSGO) map units (MUID) for all New York State swallow-wort sites and their associated soil orders and primary soil subgroups.

Map Unit Name (MUID)	Primary Soil Order	Primary Soil Subgroup	Sites	
			BSW	PSW
HUDSON-RHINEBECK-COLLAMER (NY138)	Alfisols	Hapludalfs		8
WASSAIC-FARMINGTON-LAIRDSVILLE (NY142)	Alfisols	Hapludalfs		6
HONEOYE-ONTARIO-LIMA (NY128)	Alfisols	Hapludalfs		4
ARKPORT-DUNKIRK-PALMYRA (NY078)	Alfisols	Hapludalfs		3
DARIEN-CAZENOVIA-NUNDA (NY131)	Alfisols	Endoaqualfs		3
CHAUMONT-WILPOINT-GUFFIN (NY066)	Alfisols	Endoaqualfs		3
MADRID-BOMBAY-ONTARIO (NY003)	Alfisols	Hapludalfs		1
URBAN LAND-HOWARD-NIAGARA (NY143)	Alfisols	Urban		1
RHINEBECK-KINGSBURY-HOLLIS (NY087)	Alfisols	Endoaqualfs	1	
FARMINGTON-GALWAY-STOCKBRIDGE (NY158)	Inceptisols	Eutrudepts		5
MARDIN-LORDSTOWN-VOLUSIA (NY126)	Inceptisols	Fragiudepts		2
PINCKNEY-CAMRODEN-BICE (NY037)	Inceptisols	Fragiudepts		2
IRA-SCRIBA-SODUS (NY130)	Inceptisols	Fragiudepts		1

Table 1.3 (Continued)

INSULA-ROCK OUTCROP-MUSKELLUNGE (NY146)	Inceptisols	Dystrudepts		1
CHENANGO-HOWARD-PALMYRA (NY134)	Inceptisols	Dystrudepts		1
RIVERHEAD-HAVEN-PLYMOUTH (NY103)	Inceptisols	Dystrudepts		1
CHARLTON-HOLLIS-CHATFIELD (NY157)	Inceptisols	Dystrudepts	2	1
MONTAUK-HAVEN-URBAN LAND (NY031)	Inceptisols	Dystrudepts	1	1
HOGANSBURG-GRENVILLE-MUSKELLUNGE (NY011)	Inceptisols	Eutrudepts	2	
PAXTON-WOODBRIDGE-URBAN LAND (NY028)	Inceptisols	Dystrudepts	1	
URBAN LAND-HEMPSTEAD-MINEOLA (NY161)	Inceptisols	Urban	1	
HOOSIC-WINDSOR-LIMERICK (NY149)	Inceptisols	Dystrudepts	1	
COLONIE-ELNORA-OAKVILLE (NY084)	Entisols	Udipsamments	3	1
ADAMS-COLTON-DUXBURY (NY152)	Spodosols	Haplorthods		1
URBAN LAND-UDORTHENTS-SUDBURY (NY168)	Mixed	Urban		6
SAPRISTS-FLUVAQUENTS-AQUENTS (NY115)	Mixed	Saprists		1
CARLISLE-PALMS-SCRIBA (NY113)	Mixed	Haplosaprists		1

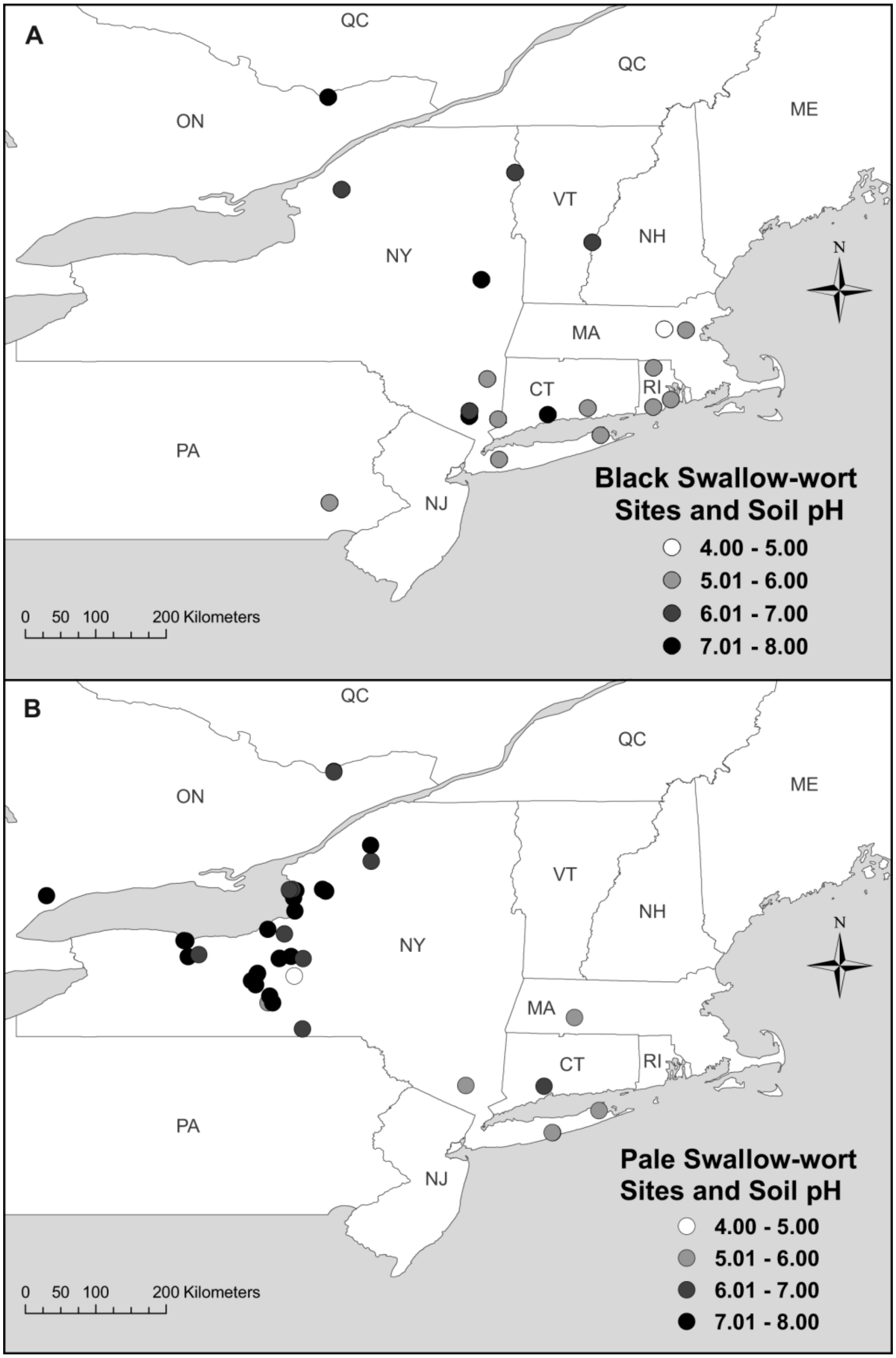

Figure 1.1. Location and soil pH of (A) black swallow-wort (n = 27) and (B) pale swallow-wort (n = 68) soil sampling sites.

agriculture that is common in the midwestern United States may have limited the western extent of the swallow-wort range in North America.This research only focused on the presence of the two swallow-wort species in the sample sites, but did not assess the relative growth or reproductive capability of these plants in the different soil samples collected. This study also did control for variations in climate, topography, land history, light availability, and swallow-wort plant density which could all have impacted swallow-wort growth and thus extent of their population size. To assess the performance of these two swallow-wort species in different soils and to control for many of the extraneous factors listed above, controlled experimentation is needed, and is addressed in Chapter 2 (Magidow et al. 2010).

In summary, we observed some differences in the type and characteristics of soils colonized by BSW and PSW and found their distributions to be distinct within NY (Figure 1.1). It is likely that soil characteristics do play some role in the current and future distribution of swallow-wort in North America. However, it is likely that the interplay between the abiotic features of habitats colonized by the swallow-worts and other factors such as their biology and ecology, time since introduction, number of introduction sites, and characteristics of their native range (Agrawal et al. 2007; Barney and Whitlow 2008) determines the distribution of these species. The swallow-worts have been present in North America since the late 1800s, but are increasingly considered troublesome plants within the last 20 years (Lawlor 2000; Milbrath and Biazzo 2006). Given the range of soils that may be suitable for colonization by the swallow-worts, all susceptible sites near existing swallow-wort populations must be carefully monitored to avoid infestation of new areas. The most at-risk habitats include minimally disturbed natural areas, trails, and roadsides.

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CHAPTER 2

EMERGENCE AND PERFORMANCE OF TWO INVASIVE SWALLOW-WORTS (*VINCETOXICUM* SPP.) IN CONTRASTING SOIL TYPES AND SOIL PH[1]

Introduction

Soil characteristics can play a key role in determining weed distributions (Dieleman et al. 2000), and in fact, soil types can be used to classify different plant communities (Firbank et al. 1990). Invasive plants display a wide range of sensitivities to soil pH, which ultimately may affect the outcome of inter-species competition (Buchanan et al. 1975; Weaver and Hamill 1985). Moreover, underlying soil and landscape characteristics can impact the success of control efforts whether based on biological (Shea et al. 2005), mechanical (Diez et al. 2009), or chemical control (Patterson 1995).

Black swallow-wort (*Vincetoxicum nigrum* (L.) Moench.) (hereafter referred to as BSW) and pale swallow-wort (*Vincetoxicum rossicum* (Kleopow) Barbar.) (hereafter referred to as PSW) are two problematic non-native invasive vines in the Apocynaceae that are spreading across eastern North America. These herbaceous perennials were introduced into North America in the mid- to late-1800s, BSW from southwestern Europe and PSW from Ukraine (Sheeley and Raynal 1996; DiTommaso et al. 2005). Despite their introduction into North America more than 150 years ago, their prevalence and spread in their new range has increased substantially during the

[1] Coauthored with Antonio DiTommaso, Quirine M. Ketterings, & Lindsey R. Milbrath.

last two decades. The current North American range of both species is climatically similar to the eastern European range of PSW, and includes the Great Lakes Basin of the northeastern United States and southeastern Ontario, Canada (DiTommaso et al. 2005; Kricsfalusy and Miller 2008). It is unclear why the North American range of BSW includes some regions that are climatically very different from that of its native southwestern European range.

In North America, the two swallow-wort species threaten a wide range of natural and semi-natural ecosystems, where they can form dense monocultures to the detriment of native plant and animal species. Also at risk are Christmas tree plantations, rights-of-way corridors, forest revegetation areas, and reduced- or no-tillage cropping systems (DiTommaso et al. 2005; Weston et al. 2005). Control of swallow-wort can be difficult and costly, often requiring repeated mechanical and chemical control (Lawlor and Raynal 2002; Mervosh and Gumbart 2006; Averill et al. 2008). A biological control effort is underway, and its success will likely depend on a more in depth understanding of the biology and ecology of these two invasive vines (DiTommaso and Milbrath 2006; Milbrath and Biazzo 2006).

Both BSW and PSW reproduce and spread primarily by wind-borne, comose seed (Cappuccino et al. 2002), although they can also spread vegetatively from the root stalk (Lumer and Yost 1995; DiTommaso et al. 2005; Averill 2009). The seed are borne in follicles, which dehisce in late summer and early fall. Although swallow-wort seeds can remain dormant in soil for 2 to 3 years, most of the seed produced in a growing season germinate and emerge the following spring (Ladd and Cappuccino 2005). At present however, it is not known to what degree propagule establishment and subsequent plant growth are affected by the soil characteristics of a new habitat.

In a recent survey of the current distribution and soil characteristics of sites occupied by BSW and PSW (Chapter 1; Magidow et al. 2010), both species were found on soils having a wide range of pH (BSW pH= 4.7 to 8.0 and PSW= pH 4.4 to 7.9). Previous observations and anecdotal information had associated BSW with low pH soils and PSW with high pH soils (Lawlor and Raynal 2002; DiTommaso et al. 2005; Douglass et al. 2009). Magidow et al. (2010) found that BSW was primarily associated with inceptisols and PSW with alfisols, although neither species appeared to be constrained to these two soil types. The current ranges of BSW and PSW in North America remain relatively distinct, with little overlap. Despite these general observations, no studies to our knowledge have assessed the effects of soil factors such as soil type and soil pH on emergence or growth of BSW and PSW in their introduced range. A more in depth understanding of how these soil factors affect the establishment and growth of these two swallow-wort species may provide valuable insight into which habitats or regions of North America may be most susceptible to future colonization by these two aggressive vines.

Using a replicated common garden experiment and a soil incubation and seed germination growth chamber study, the objective of this research was to determine whether soil type and pH affect the emergence and/or growth of BSW and PSW. We hypothesized that BSW would germinate and perform best on an inceptisol at lower pH levels (i.e. pH < 6.5) and that PSW would germinate and perform best on an alfisol at higher pH levels (pH > 7.5)

Materials and Methods

Common Garden Field Experiment. A common garden experiment was conducted in Ithaca, NY (42.5º N, 76.5 º W) to test the effects of pH and soil type on BSW and PSW emergence and growth. The research site was prepared in the summer of 2005 and the first year of the experiment spanned from August 2005 to October 2006 (henceforth referred to as Y1). The experiment was repeated for a second year, August 2006 to October 2007 (henceforth referred to as Y2). The experiment was a 3-way factorial randomized complete block design with 5 replications consisting of 12 treatment combinations: two types of soil (see description below), two swallow-wort species (BSW and PSW), and three levels of pH (defined below). In August 2005, three trenches approximately 30 m long by 1 m deep by 0.5 m wide were lined with drainage tile, which was then covered with gravel. On top of the leveled gravel, 20 23-L plastic pots[1] were placed at 0.5 m intervals in each trench (60 pots total). The space between the pots was backfilled with the surrounding soil and leveled. The within-row area was covered with black fabric mulch to suppress weeds.

Soil Collection and pH Treatments. Soil was collected from swallow-wort infested sites in Onondaga County and Orange County, NY. The Onondaga County soil (OND), colonized by PSW, is a Benson-Wassaic silt loam (Loamy-skeletal, mixed, active, mesic Lithic Eutrudept and Fine-loamy, mixed, active, mesic Glossic Hapludalf) collected near Elbridge, NY (43.0° N, 76.4° W). The Orange County soil (ORA), colonized by BSW, is a Hollis gravelly loam (a Loamy, mixed, active, mesic Lithic Dystrudept) collected at Bear Mountain State Park, NY (41.3° N, 74.0° W). The soils were chosen to represent typical sites invaded by each species with contrasting soil types, ORA representing an inceptisol and OND representing an alfisol. At each

[1] Poly-tainer™ size #7 tall. Nursery Supplies, Inc. http://www.nurserysupplies.com/

site, existing plant material and leaf litter were scraped off of the soil surface and 500 L of soil was collected to a depth of 15 cm and screened through 1.2 cm hardware cloth to remove large stones and plant roots. The soil was then transported back to the Cornell University campus in Ithaca, NY, where it was air dried in an unheated area for 3 months. After drying, the soil was homogenized in a 142-L soil mixer[2] and six samples were submitted to the Cornell Nutrient Analysis Laboratory (CNAL) to determine pH, exchange acidity organic matter (OM), and Morgan extractable, calcium, magnesium, and iron (Morgan 1941).

Our goal was to treat the soils to attain a low pH of 4.5 (pH-L), a medium pH level of 6.5 (pH-M), and high pH level of 8.0 (pH-H). Both soils had an initial median pH of 5.9 to 6.0, which was left unamended for the pH-M treatment. The soil was treated with ferrous sulfate heptahydrate[3] to achieve the pH-L treatment and with pelletized limestone[4] (Effective Neutralizing Value = 86.24%) to achieve the pH-H treatment. Both amendments were selected because of their ability to react completely with the test soils within the experimental timeline. Calculations were based on lime recommendations from Ketterings et al. (2006), and acidification recommendations from the University of Minnesota Cooperative Extension (Ducklow and Peterson 2004) (Appendix A).

*Planting, Monitoring, and Harvesting***.** Mature swallow-wort seed was gathered in August of 2005 and 2006 from plants growing at the two soil collection sites. The coma was removed from each seed and seeds lacking an embryo were discarded. In October of 2005 and 2006, each 23-L pot was filled with the appropriately treated soil and 100 seeds of either PSW or BSW were scattered by hand on the soil surface to

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[2] Twin Shell Dry Blender, Patterson-Kelley Company, Inc., East Stroudsburg, PA.
[3] Hummert International. 4500 Earth City Expressway, Earth City, MO.
[4] Graymont. Richmond, BC, Canada.

simulate seed rain and to ensure an adequate plant density given an expected minimum germination rate of 25%. During the winter months, pots were covered with 1.2-cm hardware cloth to prevent seed predation by small mammals. Swallow-wort seedlings began to emerge in late May in both years and emergence was recorded weekly for each pot throughout the growing season. Seedlings of unwanted species, such as dandelion (*Taraxacum officinale* Weber) that drifted into pots from the surrounding field, were removed by hand weekly. When plants reached 15 to 20 cm in height in late July, they were thinned randomly to 6 plants per pot to achieve a low-to-moderate density of 85 plants m^{-2} (Lawlor and Raynal 2002), minimizing intra-specific interactions. Height and node number of the selected plants were recorded at thinning. In early October, just prior to a hard frost, pots were removed from the field and brought inside for harvesting plant tissues and collecting soil samples. Soil samples were submitted to CNAL to measure the final soil pH. Each plant was cut at the soil line and plant material divided into roots, stems, leaves, and follicles, oven-dried at 50 C for 3 d and weighed to determine biomass. The following parameters were also recorded for each target plant: stem length, number of nodes, and number of follicles. Because some leaves were lost due to senescence and disturbance during harvesting, root-to-shoot ratios were calculated using stem weight only. It is possible that some swallow-wort seeds may have been present in the soil collected from the two field sites and could have germinated during the experiment. However, because the soil surface was cleared of most debris before collection (including swallow-wort seeds laying on the surface) and that the soil was subsequently mixed multiple times, the number of seeds that could have made it to the surface in the pots and germinate would be negligible and would likely be similar across treatments. Weather data for both years were obtained from the Northeast Regional Climate Center (NRCC) Ithaca Climate Page (Cornell University 2009).

Data Analysis. The Y1 calculations overestimated the sand content of ORA soil, and as a result the ORA pH-L soil did not attain its intended pH, so this treatment combination was excluded from analysis in Y1. Stem height and number of nodes were log transformed, and emergence, stem weight, root weight, root-to-stem ratio, and number of follicles per plant were square root transformed to improve normality and heterogeneity of variance. Follicle number and emergence were found to have a Poisson distribution. Each growth measurement was tested for differences between years using one-way ANOVA. The main effects in our model were species, soil type, and pH, which were included as nominal independent variables in the analysis. The measurement data were tested for correlation with each other using standard least squares regression and results were reported using Pearson's correlation coefficient. One-way ANOVA was used to test for differences in plant parameters by the main effects. Interaction effects were tested using a full factorial model and least squares regression for stem height, stem weight, number of nodes, root weight, and root-to-stem ratio and a generalized linear model with a Poisson distribution for seedling emergence and number of follicles. Stepwise regression was used to determine the best model for each growth measurement. Analysis was performed using the JMP 7.0 statistical program (SAS Institute, Inc. 2007).

Growth Chamber Soil Incubation and Germination Experiment. This experiment expanded on the common garden field experiment by providing a more controlled environment and smaller soil volumes, thus allowing us to use more pH treatments. The experiment was performed under growth chamber conditions for 18 wk (May to September 2007). The first 15 wk comprised the soil incubation component of the study (Wolf et al. 2008; Dietzel et al. 2009) and the last 3 wk comprised the germination part of the study (Noe and Zedler 2000; DiTommaso 2004). The experiment was a randomized complete block design, blocked by growth chamber, with three replicates. Treatments consisted of two soil types (OND and ORA), two swallow-wort species (BSW and PSW), and twelve pH levels (at 0.5 increments from pH = 4.0 to 9.5).

Incubation Component. The soils were air dried and samples of each soil were submitted to the Cornell Nutrient Analysis Laboratory (CNAL) to determine field water capacity, pH, exchange acidity, and plant available water. The soils were treated to achieve twelve pH levels using pulverized limestone and ferrous sulfate, according to the recommendations established by Cornell Nutrient Analysis Laboratory (Ketterings et al. 2006) and (Ducklow and Peterson 2004) and in the same manner as used in the common garden field experiment (Appendix A). Field water capacity was determined by calculating the difference between field moist weight and the air dry weight of the soil samples (Sims and Wolf 1995). A total of 100 g of each soil-pH combination were placed into 355 mL Styrofoam deli cups. Deionized water was added to each soil container to attain field water capacity, and the contents stirred and gently leveled. Containers were covered with perforated lids and placed in an unlit growth chamber set at a constant temperature of 20 C. During the next 15 wk, the soil was subjected to five 3-wk cycles of two weeks covered incubation at field capacity, and one week of evaporation with lids removed. Between cycles, soils were rewetted to field capacity and the soil was stirred and leveled. After 15 wk, the soil was removed from the cups and oven-dried for three days at 32 C.

Germination Component. Mature swallow-wort seeds were collected in late summer and early fall of 2006 from the same sites as the soil used for the incubation component of the study. The coma was removed from the seed, and the seed were kept in dry cold storage (3-5 C) until spring 2007. Seed were weighed and those lacking embryos were discarded. At week 3 of the soil incubation experiment, 1000 seed of each species were placed on moist germination paper and cold-stratified at 3-5 C for

12 wk. At week 10, seed were tested for viability by randomly selecting 100 seed of each species and placing on wet germination paper in a growth chamber kept at 25/17 C (day/night) temperature and 14/10 h photoperiod. After one week, the percentage of seeds germinating was determined. The seed for replicates 1 and 2 were harvested in August 2006 and had viability rates of 88% and 86% for PSW and BSW, respectively. The seed for replicate 3 were collected in October 2006 and had viability rates of 100% for PSW and 93% for BSW. When the soil incubation was complete, 90 g of soil of each type and pH level was placed into 150 mL clear plastic beverage containers[5] and brought to field water capacity. Each container was sown with ten seed of PSW or BSW to a depth of 0.6 cm. The containers were placed into three different growth chambers kept at 25/17 C temperature and 14/10 h photoperiod for 21 d. The three replicates were blocked by seed source and growth chamber. Cups were watered every other day to maintain their moisture level within 20% of field capacity and re-randomized within the growth chamber. Emerged seedlings were removed from the cups and counted daily. At 21 d, the soil was air-dried at 32 C, crushed and passed through a 2mm sieve, and the final pH in a 1:1 soil:water ratio (w:v) was tested using a Fisher computer aided titrimeter (Sims and Wolf 1995).

Data Analysis. The response variables for the germination trial were percentage of seed that germinated after 21 d, days to 50% germination, and germination speed. Germination speed was determined using the index below:

$$\sum n_{\mathrm{t}}/(n_{\mathrm{f}}\mathrm{t})$$

[5] Covalence Plastics, Minneapolis, MN.

where n_t is the cumulative proportion of seeds that had germinated by a given sampling day of the experiment, n_f is the cumulative proportion of seeds that germinated at the end of the experiment (21 d), and t is the sampling day (t = 1, 3, 5,..., 21). The sum of index values for the duration of the study is the total germination speed index, a value between 0 and 1. Seeds that germinated sooner had a higher index value than those that germinated later (Noe and Zedler 2000). Proportion of total germination and germination speed index were transformed using the arcsine square root transformation, and days to 50% germination was transformed using the natural log to improve normality and heterogeneity of variance. The main factors: soil type, species, and pH were evaluated as parameters affecting proportion of total germination, germination speed index, and days to 50% germination using stepwise multiple regression to determine the optimal regression model given these independent and dependent variables. The response variables were evaluated to determine if they varied by treatment factor using one-way ANOVA with $\alpha = 0.05$. The data were analyzed using the JMP 7.0 statistical program (SAS Institute, Inc. 2007).

Results and Discussion

Common Garden Field Experiment. Soil pH for the pH-L treatment did not change over time after the soil overwintered in the field in both years. The median pH for pH-H in Y1 remained close to 7.3 throughout the season. At the beginning and end of the growing season in Y2, the median pH for the pH-H treatment was 7.2, but decreased to 6.8 for both soils during July. This decrease in pH coincided with heavy rainfall late in the season, which may have temporarily decreased the pH due to leaching.

Leaching is partially offset by plant uptake, which may explain why the pH returned to treated values as the plants matured and limestone particles continued to react in the soil (Troeh and Thompson 1993).

Seedling Emergence. The only parameter which differed by year was the number of seedlings emerged by the third week of July ($P < 0.0001$). Emergence in Y1 (2007) (mean ± SE, 39.6 ± 0.3) was more than double that in Y2 (2008) (14.6 ± 0.2). Weather differences prior to the thinning of seedlings in the two years may have affected results. Year 1 of the study was slightly warmer and much wetter than Y2, which was closer to the 30-yr average conditions (Table 2.1). In Y1, emergence was greater on OND soil ($P < 0.001$) (Figure 2.1), although emergence did not differ in Y2. In both years, PSW had greater emergence than BSW ($P < 0.0001$) (Figure 2.2).

Differences in emergence between the two species may have been due to inherent seed size differences as seeds of BSW are much larger (10-26 mg) than PSW (2-9 mg) seeds. As primarily wind-dispersed species, swallow-wort seeds can reach a wide array of environments that may or may not be hospitable to their establishment. In general, large seeds can more easily germinate and seedlings establish under more stressful conditions such as shade or deep burial (Leishman et al. 2000) than smaller seeds (Kidson and Westoby 2000). In the relatively low-stress and negligible competitive conditions present in this experiment, the smaller-seeded PSW was able to germinate and establish seedlings more rapidly than BSW. Differences in the rate of germination and establishment between the two species in heterogeneous environments will likely impact the future range of the two swallow-wort species,

Table 2.1. Average monthly temperatures, total precipitation, and growing season data in 2005, 2006, 2007 and the 30-year average (1976-2006) for a weather station located 3 km from the common garden field site in Ithaca, NY.

	Temperature				Precipitation			
Month	2005	2006	2007	30-yr	2005	2006	2007	30-yr
	C				mm			
January	-6.6	-0.1	-2.1	-5.2	108.7	70.1	60.2	53.8
February	-3.8	-2.4	-8.7	-4.7	55.9	36.3	51.1	52.3
March	-2.3	-0.5	-1.2	0.2	62.2	46.0	89.2	65.0
April	7.9	7.3	5.1	6.6	116.3	45.2	87.6	83.6
May	10.4	12.9	13.2	13.0	34.5	62.2	23.6	81.8
June	21.1	18.2	19.0	18.0	138.4	191.0	73.2	98.3
July	22.4	21.9	19.4	20.4	34.3	172.0	121.4	89.9
August	21.9	19.7	20.2	19.6	71.1	122.9	72.6	86.1
September	17.2	15.1	17.2	15.2	53.6	67.3	107.7	97.5
October	10.0	8.3	13.4	9.1	184.7	108.0	85.9	82.0
November	6.3	6.0	3.2	3.8	109.2	73.9	106.2	78.7
December	-3.9	2.3	-2.1	-2.1	51.6	46.2	92.2	63.2
Annual total					1020.6	1041.1	970.8	932.4
Monthly average	8.4	9.1	8.1	7.8	85.0	86.8	80.9	77.7
Growing season average/total (April-October)	15.8	14.8	15.4	14.6	90.4	109.8	81.7	88.5

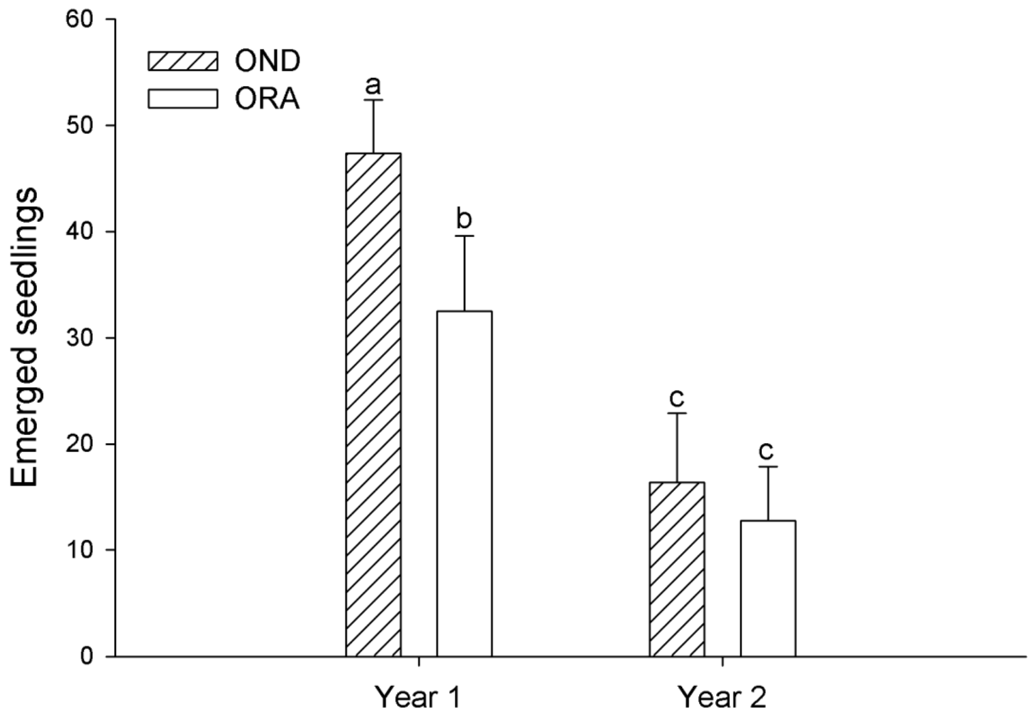

Figure 2.1. Mean emergence of swallow-wort (+95% CI) by late July in Year 1 (n = 40, $P < 0.0001$) and Year 2 (n = 60, $P = 0.3297$) as affected by soil type in a common garden field experiment. Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, $P < 0.05$).

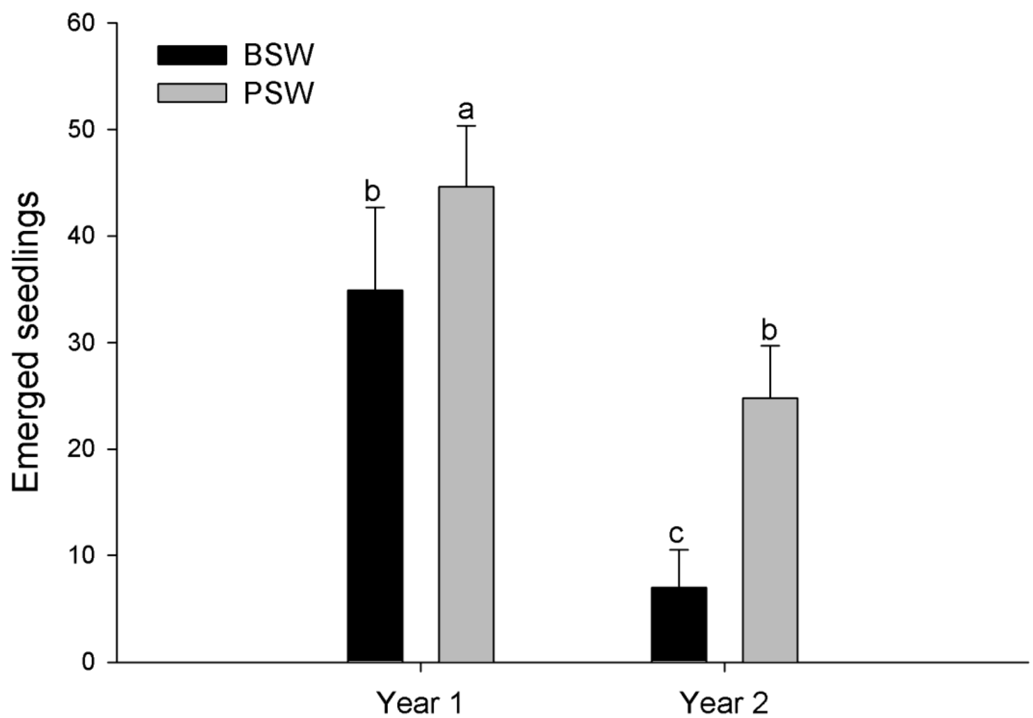

Figure 2.2. Mean emergence of swallow-wort (+ 95% CI) by late July in Year 1 (n = 40, $P = 0.0382$) and Year 2 (n = 60, $P < 0.0001$) as affected by species in a common garden field experiment. Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, $P < 0.05$).

although few comparative studies using these two species have been performed (e.g. Milbrath 2008; Ho 2009; Magidow et al. 2010).

Soil pH had no effect on emergence in either year. Soil type and species interacted to affect seedling emergence in Y1 ($P < 0.0001$) (Figure 2.3), with low BSW emergence on ORA soil and similar emergence levels for the other treatment combinations. The greater soil water-holding capacity (30.7% at 33 kPa) of the OND soil compared with the ORA soil (17.1% water at 33 kPa) may explain the higher emergence of swallow-wort seedlings on OND soil. It is also possible that the colder winter temperatures experienced in Y2 compared with Y1 may have caused more seed death in Y2 and thus resulted in lower seedling emergence for both swallow-wort species, but especially BSW. It is worth noting that the climatic conditions in PSW's native Ukraine are similar to conditions generally found in its introduced range in the northeastern U.S., while BSW's native southwestern European range is considerably drier than the northeastern U.S. introduced range (546-708 mm compared with 932 mm annual rainfall) (DiTommaso et al. 2005).

Approximately 50% of PSW and 30% of BSW seeds exhibit polyembryony, a condition that gives rise to multiple seedlings (2-3, rarely 4+) from a single seed (Sheeley and Raynal 1996; Smith et al. 2006; Hotchkiss et al. 2008). First-year swallow-wort emergence rates for surface-sown seeds have been observed to range from 2 to 20% (Averill 2009) and 38.4% (Ladd and Cappuccino 2005). Much higher rates (~80%) have been observed under growth chamber conditions (L. Magidow, Cornell University, unpublished data). Averill (2009) and Hotchkiss et al. (2008) showed that polyembryony did not affect seedling emergence, but Ladd and Cappuccino (2005) reported that polyembryony did increase plant survivorship past one year. Hotchkiss et al. (2008) reported seedling survival over 3 years to be 20-60% and Averill (2009) observed a wide range of survival over two years, from 0-100%.

Although care was taken in our study to note if multiple seedlings emerged from the same polyembryonic seed, emergence could have been slightly overestimated if several shoots arose from the same seed. Polyembryony was observed to be very low (< 5%), but was difficult to detect without destroying the seedlings. In her 2-yr field study, Averill (2009) found only 4% of PSW seedlings to be polyembryonic, whereas Cappuccino et al. (2002) reported polyembryony levels as high as 55%, and Sheeley

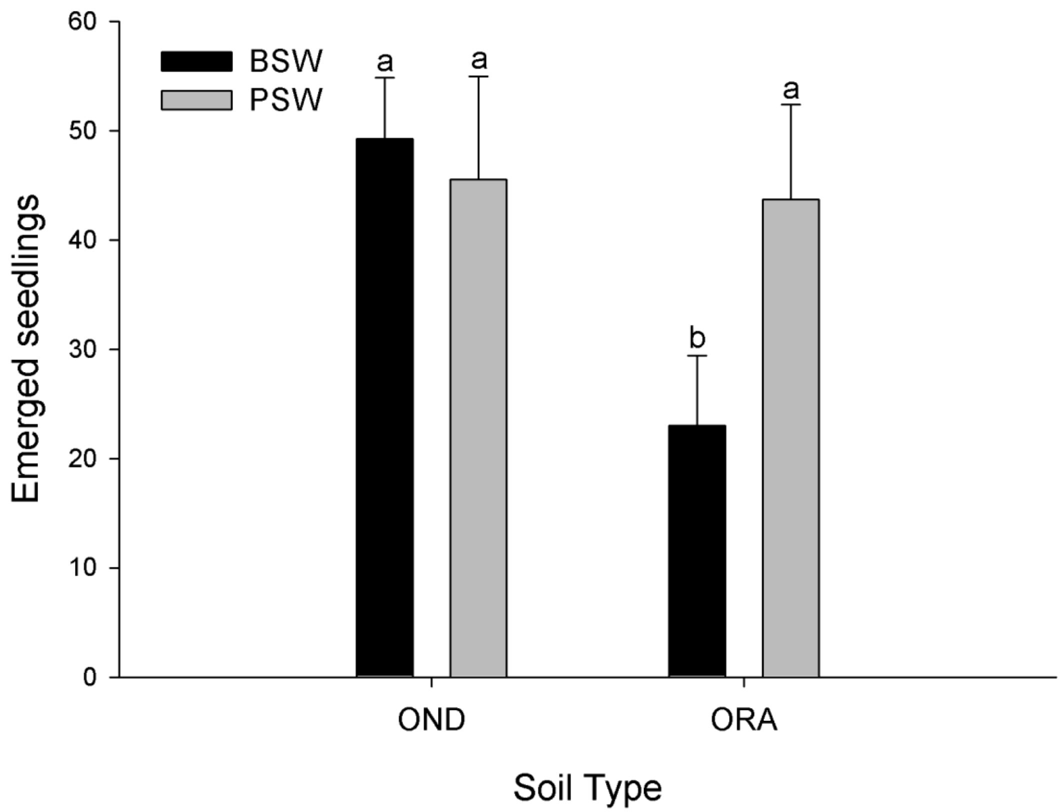

Figure 2.3. Mean seedling emergence (+ 95% CI, $P < 0.0001$) as affected by soil type and species interaction in Year 1 of a common garden experiment (n = 40). Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, $P < 0.05$).

(1992) observed 78% of seeds to be polyembryonic under greenhouse conditions. Once plants were thinned to 6 plants per pot, any additional polyembryonically-derived seedlings present were removed.

Aboveground Growth. Growth data for Y1 and Y2 were combined for all remaining analyses. Species was the best predictor of aboveground biomass, with BSW exhibiting greater height, stem biomass, number of stem nodes, and number of plants with follicles than PSW plants across all soil type and pH combinations (Table 2.2). The more vigorous aboveground growth of BSW relative to PSW is consistent with recent observations by Milbrath (2008) and Ho (2009). In our study, four times as many BSW plants produced follicles as PSW plants ($P < 0.0001$) after one growing season (Table 2.2). In general, BSW has been observed to reproduce earlier than PSW in both greenhouse and common garden conditions (Milbrath 2008; L. Magidow, personal observation). In fact, McKague and Cappuccino (2005) reported that no PSW plants originating from seed had flowered after four growing seasons in Ontario, Canada.

Table 2.2. Mean (± SE) values per plant for various growth parameters measured for two swallow-wort species in a common garden experiment (n = 100, unless otherwise noted). Means having the same letter within a row are not significantly different (Tukey-Kramer's HSD test, $P < 0.05$). Root-to-stem ratio values are based on dry biomass of stem only, leaves excluded.

	Black swallow-wort				Pale Swallow-wort			
Parameter	Mean		SE		Mean		SE	
Stem height (cm)	27.83	±	0.05	a	20.39	±	0.05	b
Stem weight (g)	0.08	±	0.02	a	0.12	±	0.02	b
No. stem nodes	13.19	±	0.02	a	10.81	±	0.02	b
No. plants with follicles	0.61	±	0.08	a	0.12	±	0.08	b
Root weight (g)	2.35	±	0.05	a	2.08	±	0.05	a
Root-to-stem ratio	12.39	±	0.11	a	18.85	±	0.11	b

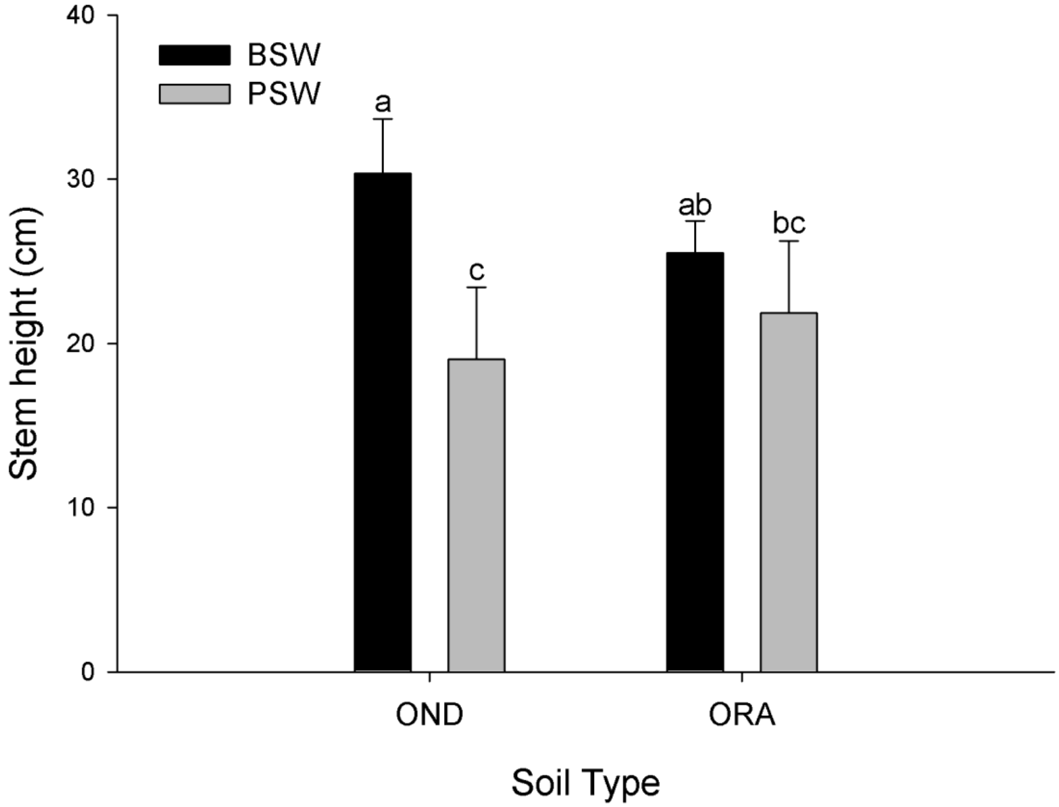

Figure 2.4. Mean stem height (+ 95% CI, *P* < 0.0001 as affected by swallow-wort species and soil type (n = 100). Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, *P* < 0.05).

There was a highly significant (*P* < 0.0001) soil type by species interaction on stem height, with both BSW demonstrating the greatest height and PSW the least height on OND soil (Figure 2.4). In contrast, stem height did not differ by swallow-wort species on the ORA soil. This result is not consistent with our hypothesis that each species would grow best on its associated soil (i.e. ORA for BSW and OND for PSW). However, differences in these stem height results may have little impact for the spread of swallow-wort, as we observed little difference in the production of follicles by the two swallow-wort species in the two soil types. Given that BSW and PSW may colonize both alfisols and inceptisols (Chapter 1; Magidow et al. 2010), findings from this common garden study suggest that both species once on these two soils can grow relatively well.

Belowground Growth. In contrast to aboveground parameters, root weight did not differ by swallow-wort species but it did differ by pH treatment. Root weight was lowest in the pH-L (median pH = 5.4) treatment but did not differ between the pH-M (pH = 6.1) and pH-H (pH = 7.3) treatments (Figure 2.5). The maximum pH value we achieved in our study is within the range favorable for growth of most plants (Brady and Weil 2002). However, if the pH-H treatment had attained a more extreme pH value, we may have observed some differences in growth between the two species, although both swallow-worts have been found growing on soils with a pH value as high as 8.0 (Chapter 1; Magidow et al. 2010). Despite root weight being lower in the pH-L soils, aboveground growth was not affected by the pH treatment, indicating that both species were able to grow well despite reduced root growth in this pH soil treatment. The root-to-stem ratio was not affected by soil type or pH treatment and differed only by species ($P < 0.0001$) with PSW having a greater root-to-stem ratio than BSW (Table 2.2). This relatively high investment of PSW plants into belowground structures is consistent with results from several other studies using this species (DiTommaso et al. 2005; Milbrath 2008; Ho 2009; Averill 2009).

Findings from this common garden study suggest that these two invasive vines may be employing different competitive strategies to colonize and dominate new sites early on—with PSW emphasizing belowground growth while BSW invests more resources into aboveground structures and sexual reproduction. These different resource allocation strategies are consistent with recent work showing that PSW has a greater ability to colonize a variety of environments, from open sunny habitats to heavily shaded forest understories, likely because of its relatively high investment of resources into belowground structures (Hotchkiss et al. 2008). For example, Milbrath(2008) found that under high light conditions in a greenhouse, BSW had greater aboveground biomass, longer stems, and greater follicle production and that

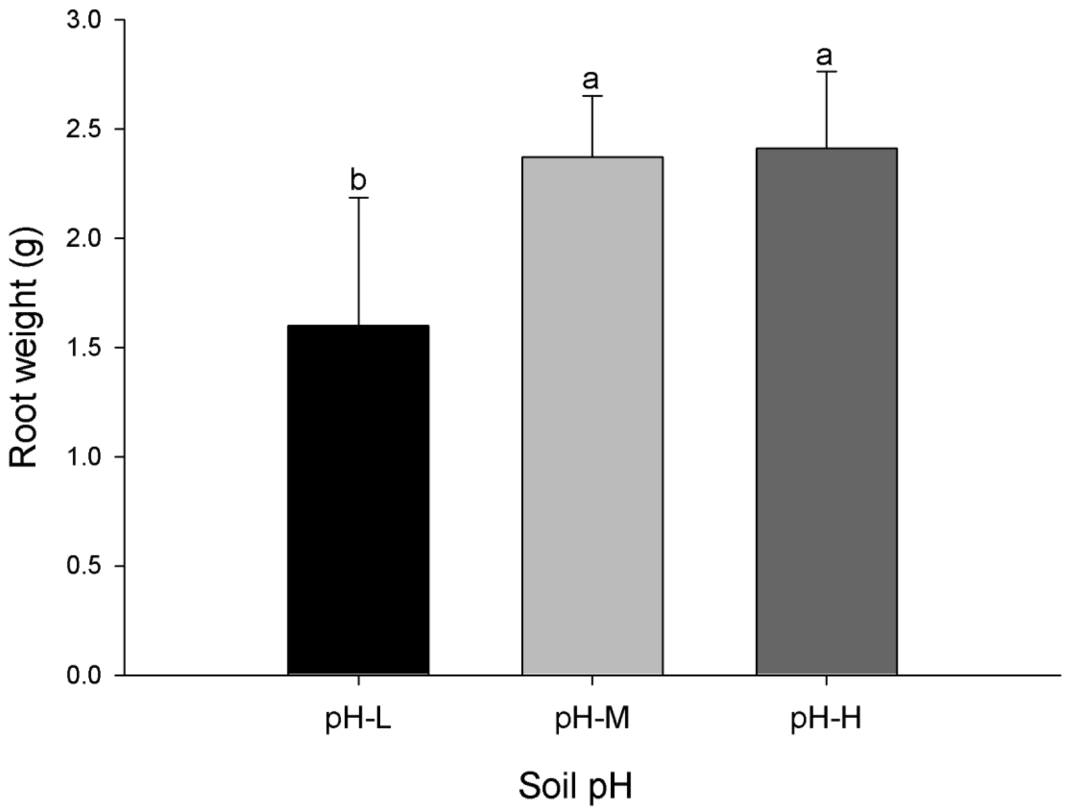

Figure 2.5. Mean swallow-wort root weight (+95% CI, P<0.0065) as affected by soil pH treatment in a common garden experiment (n = 100). Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, $P < 0.05$).

PSW had a greater root biomass and root-to-shoot ratio. However, under low-light conditions, there was no difference in aboveground biomass or root-to-shoot ratio between the two swallow-wort species. Given that our common garden experiment was carried out under the high-light conditions typical of open, early successional fields in the northeastern U.S., it may have favored the performance of BSW relative to PSW. It is likely that the performance of the two species could have varied had our study been performed under the low-light conditions more typical of shaded understories.

Incubation and Germination Experiment. The soil incubation achieved a minimum pH of 4.7 and a maximum pH of 7.4. Final mean germination after 21 d was 68% for all species, soil type, and pH treatments combined. In 75% of containers over 50% of seeds had germinated and in 25% of containers over 90% of seeds had germinated during the 21-d experimental period. The median number of days to 50% germination did not differ between PSW (9 d) and BSW (11 d). Moreover, rate of germination did not differ by species, soil type, or pH. However, a greater final proportion of seeds germinated in the OND soil relative to the ORA soil (P = 0.0205) (Figure 2.6). The lower germination we observed on the ORA soil is likely due to its sandier texture, and lower field water capacity (17.1% water at 33 kPa) compared with the OND soil (30.7% at 33 kPa). The growth differences between the two swallow-wort species observed in the common garden experiment were not observed in this growth chamber experiment. However, under controlled growth chamber conditions germinated seedlings were allowed to grow to 1-2 cm in height prior to measurements being taken, whereas seedlings in the field experiment appeared more robust and grew to 3-5 cm height before being counted. Therefore, species differences may not become apparent until seedlings are older and develop under more stressful conditions than was the case in our controlled growth chamber study.

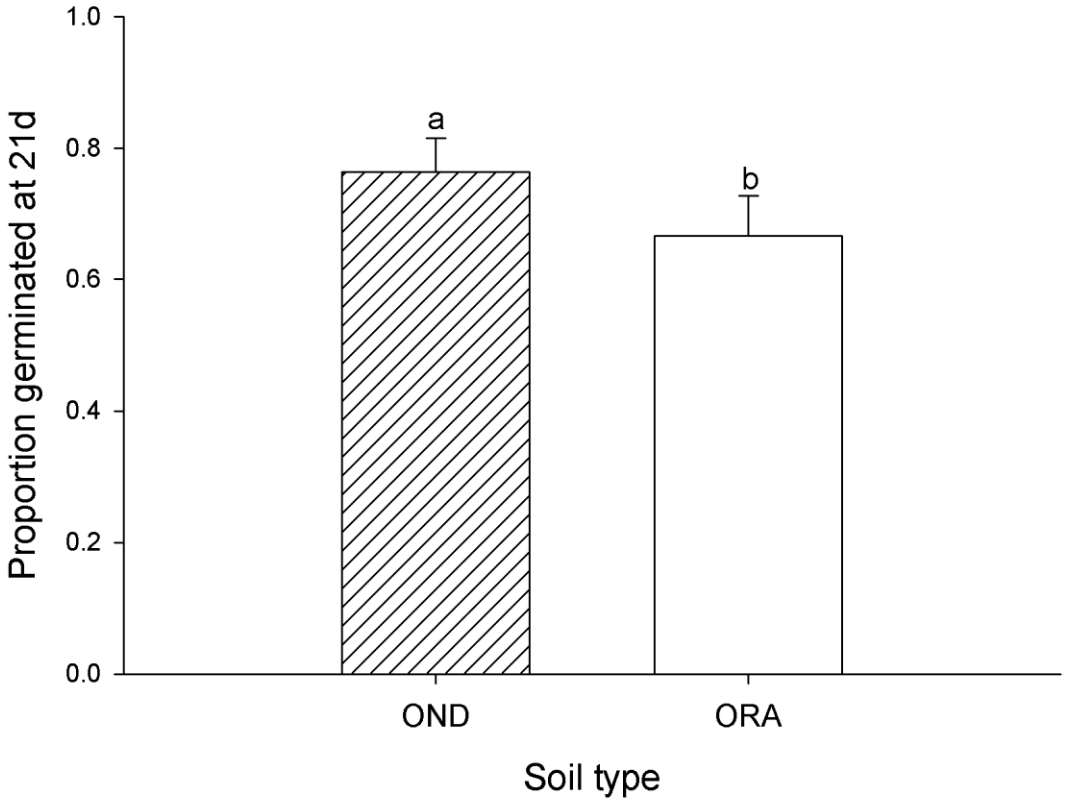

Figure 2.6. Mean proportion of swallow-wort seed germinated at 21 days after planting (+ 95% CI, $P = 0.0205$) as affected by soil type in a soil incubation and growth chamber experiment (n = 144). Bars denoted by the same letter are not significantly different (Tukey-Kramer's HSD test, $P = 0.05$).

We hypothesized that the growth of the two swallow-wort species would differ and be influenced by soil type and soil pH. There were substantial differences between the two species for most parameters measured in the field, although these differences were not evident in very young seedlings in the growth chamber environment. Soil type had some impact on swallow-wort emergence and growth, but the inclusion of additional soil types in future studies will greatly enhance the general applicability of our findings. More research is needed to determine if and how much of a role soil type plays in the distribution of the two swallow-wort species in their introduced North American range. Contrary to anecdotal information, soil pH had a minimal effect on swallow-wort growth parameters measured, and given the wide range of soil pH values found at swallow-wort colonized sites (Chapter 1; Magidow et al. 2010), it is unlikely that soil pH alone plays a significant role in the distribution of these species in its introduced range. Weed species vary in their dependence on soil pH for growth (Buchanan et al. 1975) and it appears that BSW and PSW are relatively pH-insensitive species. In all pH treatments, a high number of both swallow-wort species germinated and emerged, produced substantial above-and belowground biomass, and produced at least some seed-bearing follicles. Therefore, we conclude that the current and future North American distribution of these two invasive vines is not limited by soil pH, or by the two soil types we examined. Rather, their distribution will likely be determined by other factors such as number and location of introductions, seed dispersal, habitat disturbance, or water drainage and light availabilities of potential sites. At present, it remains unclear whether the introduced ranges of BSW and PSW will eventually overlap, but, despite its limitations, results from our study suggest that soil types or pH levels are likely not to limit the range expansion (and overlap) of these two swallow-wort species.

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APPENDIX

Liming calculation:

$$Lime_{100\%\ ENV}\left(\frac{tons}{a}\right) = \frac{EA(0.05)(BS_{desired} - BS_{original})}{1 - BS_{original}}$$

Where EA = exchange acidity (meq/100 g soil), BS = base saturation (fraction). For soils with pH > 6.1, EA is replaced with cation exchange capacity (CEC, $cmol_c$/kg). Desired BS and estimated CEC for each soil obtained from Ketterings et al. (2006).

Acidifying calculation: Elemental sulfur application rates to lower soil pH by one unit (Ducklow and Peterson 2004). To convert to iron sulfate, multiply by 6. Amount of elemental sulfur to apply by area basis: $8\ lb/1000\ ft^2$ for sand, loamy sand, or sandy loam; $24\ lb/1000\ ft^2$ for loam or silt loam. The results can be converted to pounds per acre using $lb/1000\ ft^2\ \times 44 = lb/a$. Amendment rates for the field and growth chamber experiments were calculated as follows:

$$FeSO_4 \cdot H_2O(lbs/lb_{soil}) = \left(\frac{24\ lbs}{ft^2}\right)\left(\frac{44\ ft}{a}\right)(6)(\ units\ pH)\left(\frac{1\ acre}{2\ \times 10^6}\right)$$